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How geographic productivity patterns affect food-web evolution

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ABSTRACT

It is well recognized that spatial heterogeneity and overall productivity have important consequences for the diversity and community structure of food webs. Yet, few, if any, studies have considered the effects of heterogeneous spatial distributions of primary production. Here, we theoretically investigate how the variance and autocorrelation length of primary production affect properties of evolved food webs consisting of one autotroph and several heterotrophs. We report the following findings. (1) Diversity increases with landscape variance and is unimodal in autocorrelation length. (2) Trophic level increases with landscape variance and is unimodal in autocorrelation length. (3) The extent to which the spatial distribution of heterotrophs differ from that of the autotroph increases with landscape variance and decreases with autocorrelation length. (4) Components of initial disruptive selection experienced by the ancestral heterotroph predict properties of the final evolved communities. Prior to our study reported here, several authors had hypothesized that diversity increases with the landscape variance of productivity. Our results support their hypothesis and contribute new facets by providing quantitative predictions that also account for autocorrelation length and additional properties of the evolved communities.

1. Introduction

To understand the complexity of organic life, scientists study the patterns and dynamics of nature through different organizational lenses, such as how life is organized across geographical space (Dieckmann et al., 2000; Kareiva, 1994; Tilman and Kareiva, 1997; Vinatier et al., 2011) and in networks of species interactions (Cohen et al., 1990; Ings et al., 2009). While the factors seen through these lenses have mainly been considered in isolation, the importance of understanding their interplay is increasingly recognized (Amarasekare, 2008; Calcagno et al., 2011; Holt, 2002; Pillai et al., 2011). Additionally, to persist for long periods of time this organizational complexity should be stable against evolutionary change, as natural selection shapes communities (Edwards et al., 2018). The interplay of all three factors—namely geographical structure, biotic interactions, and evolution—is likely to be important for the generation and maintenance of biological diversity.

Although the importance of greater integration of all three factors has been recognized (Urban et al., 2008), they are rarely considered in concert (Moya-Laraño et al., 2014; but see that study and Allhoff et al., 2015). Even fundamental questions that have received much attention in nonspatial settings have only rarely been studied in spatial, eco-evolutionary settings. One such question is how primary production affects community structure. While several authors have investigated how overall productivity affects community structure (Adler et al., 2011; Cusens et al., 2012; Mittelbach et al., 2001), it is much less studied how geographically varying levels of primary production affect biological diversity and community structure. Understanding how geographic variability affects the ecology and evolution of communities is of central importance as conditions in nature are rarely, if ever, homogeneous.

Theoreticians have already constructed a well-established literature for any two of the given three factors above. The interplay of evolution and trophic interactions, and what type of evolutionarily stable communities can form under different circumstances has been studied in spatially homogeneous settings in several models originating with the work of Loeuille and Loreau (2005) (reviewed in Fritsch et al., 2019), where the body sizes of organisms are under selection in a size-structured trophic network. These models, being mostly based on Lotka-Volterra interactions, typically exhibit increasingly diverse communities in longer food chains as the pro-

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ductivity of the basal autotroph becomes greater. The interplay of evolution and spatial structure on the other hand is known to increase diversity through local adaptation, leading to more diverse communities for more heterogeneous environments (Norberg et al., 2012; Wickman et al., 2017). Taking spatial, evolutionary, and trophic interactions into account, this then begets the question whether the most diverse food webs form when productivity is concentrated in space, allowing longer food chains to form, or when productivity is distributed in a patchy way in which the possibility of local adaptation is maximized.

In this paper, we study how different spatial configurations of primary production affect the community structure of evolutionarily stable communities. We do so by extending an eco-evolutionary size-structured food-web model by Brännström et al. (2011) to a spatially explicit setting. In this model several heterotrophs are under selection through trait (size) mediated predation and competition, while in the meantime consuming a single size-fixed primary autotrophic producer with spatially varying productivity over a landscape. We quantify two key properties of the spatial distribution of primary production, the first being its overall variability, quantified by its variance, and the second being its patchiness, quantified by autocorrelation length (ACL). Using these two properties, we determine which productivity distributions yield diverse food webs. We then investigate how this diversity is structured, by determining which productivity distributions yield food webs with high trophic levels, and how different distributions yield different spatial arrangements of heterotrophs in the food web. Finally, to compare our results with studies on evolutionary branching in heterogeneous environments, we investigate the extent to which properties of the fully evolved community can be predicted from components of disruptive selection for the ancestral heterotroph in the food web.

2. Methods and model

To investigate how geographic variability in primary production affects properties of evolved communities, we first randomly generate resource landscapes that govern the local productivity of an autotroph. We describe the variation of the resource landscape in terms of its variance and autocorrelation length (ACL). We then evolutionarily assemble a food web for each landscape starting from a single heterotroph with body size as an evolvable trait. Finally, we statistically investigate properties of the resulting evolutionarily stable communities and relate them to the variance and ACL of the resource landscape.

2.1. Ecological dynamics

We extend the evolutionary food-web model by Brännström et al. (2011) to a spatial setting, by assuming that the ecological dynamics take place on the unit square $\Omega = [0,1]^2$ with periodic boundary conditions. The model consists of one autotroph with density $u_0(\mathbf{x})$ and S heterotrophs with respective densities $u_i(\mathbf{x})$, $i = 1,2,\dots,S$, with $\mathbf{x} = (x_1, x_2)$ representing the spatial coordinates in the square. We characterize the autotroph and each heterotroph by the logarithm of the ratio of its body size to that of the autotroph $r_i = \log(s_i/s_0)$, in which s_i is the body size of the heterotroph under consideration for $i \geqslant 1$ and s_0 is the body size of the autotroph. The model is generic and is not intended to represent any specific natural system, and the morphs that evolve in the model are to be taken as functional ecological groups, rather than specific species (c.f., trait-based ecology, Litchman and Klausmeier, 2008). Nonetheless, the geometric scaling between morph sizes is likely more representative of aquatic rather than terrestrial systems, with phytoplankton serving as the autotroph. The equations describing the ecological dynamics of the food web are given by

$$\frac{\partial u_i(\mathbf{x},t)}{\partial t} = -\overbrace{d(r_i)u_i}^{\text{respiration}} + \overbrace{\sum_{j=0}^{S} e^{-r_i}\lambda e^{r_j} M_\gamma \gamma(r_i - r_j) u_j u_i}^{\text{consumption}} - \underbrace{\sum_{j=1}^{S} M_\gamma \gamma(r_j - r_i) u_j u_i}_{\text{predation}} - \underbrace{\sum_{j=1}^{S} M_\alpha \alpha(r_i - r_j) u_j u_i}_{\text{competition}} + \underbrace{D(r_i)\Delta u_i}_{\text{diffusion}}, \tag{1a}$$

$$\frac{\partial u_0(\mathbf{x},t)}{\partial t} = \underbrace{g(\mathbf{x})\left(1 - \frac{u_0}{K(\mathbf{x})}\right)u_0}_{\text{growth}} - \underbrace{\sum_{j=1}^{S} M_\gamma \gamma(r_j - r_0) u_j u_0}_{\text{predation}} + \underbrace{D(r_0)\Delta u_0}_{\text{diffusion}}, \tag{1b}$$

$$u_j(1,x_2) = u_j(0,x_2), \quad u_j(x_1,1) = u_j(x_1,0), \quad j = 0,1,2,\dots,S. \tag{1c}$$

Here, Eq. (1a) describes the dynamics of heterotroph i. The first term $d(r_i) = d_0 e^{-d_s r_i}$ describes losses due to respiration. The second term describes biomass intake by consumption of the autotroph and other heterotrophs. In this term, λ is the conversion efficiency, M_γ the predation intensity, and $\gamma(r_i - r_j) = 1/\left(\sqrt{2\pi}\sigma_\gamma\right)\exp\left[-\left(r_i - r_j - \mu_\gamma\right)^2/\left(2\sigma_\gamma^2\right)\right]$ is the predation kernel, for which the prey trait that maximizes the attack rate of a heterotroph with trait r_i is $r_j = r_i - \mu_\gamma$. Note that although μ_γ is the difference in trait between predator and prey that maximizes the attack rate, the food web may evolve in such a way that an evolutionarily stable community may have a different characteristic trait difference between heterotrophs due to the other trait-mediated terms in Eq. (1a) that govern the heterotroph dynamics (Brännström et al., 2011). The factor $e^{-r_i}e^{r_j}$, which is equal to the size ratio s_i/s_j, accounts for the difference in body mass between the consumer and the prey. The third term describes the losses due to predation from all other heterotrophs on heterotroph i. The fourth term describes losses due to interference competition, where M_α is the competition intensity, and $\alpha(r_i - r_j) = 1/\left(\sqrt{2\pi}\sigma_\alpha\right)\exp\left[-(r_i - r_j)^2/(2\sigma_\alpha^2)\right]$ is the competition kernel, where competition is the most intense between heterotrophs of the same size. The fifth term $D(r_i)\Delta u_i = D_0 e^{D_s r_i}\Delta u_i$ describes the random movement of heterotrophs, as modeled by a diffusion term, where Δ is the two-dimensional Laplacian (see, e.g., Britton, 1986; Cantrell and Cosner, 2004; Vinatier et al., 2011, for introductions to reaction–diffusion spatial models). We let the exponent for the diffusion rate be a positive number, implying an allometric scaling in the diffusion rate, with bigger heterotrophs diffusing faster (Peters, 1983). All trophic and competitive interactions are local in space.

Eq. (1b) describes the autotroph dynamics at each point in space, where the first term describes the logistic growth of the autotroph in the absence of predation. The intrinsic growth rate $g(\mathbf{x})$ and carrying capacity $K(\mathbf{x})$ vary in space depending on a randomly generated resource landscape $L(\mathbf{x})$, so that $g(\mathbf{x}) = g_0 L(\mathbf{x})$, and $K(\mathbf{x}) = K_0 L(\mathbf{x})$. How we generate this landscape is described in Section 2.2. The second term describes losses due to predation from the heterotrophs, and the third term describes the random movement of the autotroph. Eq. (1c) means that boundary conditions are periodic in both spatial coordinates.

The state variables and parameters are summarized in Table 1. We chose the values of the parameters corresponding to the nonspatial food-web model to coincide with the base case treated for the nonspatial model in Brännström et al. (2011). We made this choice to facilitate comparisons between the nonspatial and spatial model. The baseline level of diffusion D_0 will heavily influence the number of heterotrophs in the assembled community, with D_0 being small resulting in more heterotrophs, as they are able to

Table 1
Parameters and state variables in the food-web model.

Symbol	Meaning	Value/ range	Unit
u_0	Density of the autotroph		area^{-1}
u_i	Density of heterotroph i		area^{-1}
r_i	Trait value of heterotroph i		–
d_0	Baseline respiration rate	0.1	time^{-1}
d_s	Respiration scaling coefficient	0.25	–
λ	Conversion efficiency	0.3	–
M_γ	Predation intensity	10	time^{-1}
μ_γ	Prey-trait difference maximizing attack rate	3	time^{-1}
σ_γ	Predation kernel width	1.5	–
M_α	Competition intensity	1	time^{-1}
σ_α	Competition kernel width	0.6	–
D_0	Baseline diffusion rate	$5 \cdot 10^{-6}$	area time^{-1}
D_s	Diffusion scaling coefficient	0.25	–
g_0	Baseline autotroph growth rate		time^{-1}
K_0	Baseline autotroph carrying capacity		area^{-1}
t	Time		time
x_1	Horizontal spatial coordinate	$[0, 1]$	length
x_2	Vertical spatial coordinate	$[0, 1]$	length

adapt to smaller local patches (c.f., Wickman et al., 2017). Conversely, as the baseline diffusion rate becomes very large ($D_0 \to \infty$), we recover the nonspatial model on the regional scale. We have hence chosen D_0 to be at a level to provide a range of different communities without becoming numerically intractable as a result of a large number of heterotrophs. We also investigate two additional sets of nonspatial parameters to confirm the robustness of our results (see Appendix D).

We solve the partial differential equations numerically by using the method of lines and discretizing space with so-called pseudospectral methods (Trefethen, 2000). We use two ordinary differential equation solvers, ode15s and ode45, in Matlab 2016b (Mathworks, 2016) to solve the resulting semi-discretized system. A more detailed description of our numerical implementation is given in Appendix A.

2.2. Landscape generation

We randomly generate two-dimensional resource landscapes on the unit square under the assumption of periodic boundary conditions in both directions. Each landscape is described by a function $L(\mathbf{x})$ which takes a real, positive value at each point $\mathbf{x} = (x_1, x_2)$ on the square $\Omega = [0, 1]^2$ and is generated using Perlin noise (Perlin, 1985; see Appendix A). To investigate how different resource landscapes alter evolutionary outcomes, we focus on two key characteristics of the resource landscapes: landscape variance and landscape autocorrelation length (ACL). The landscape variance is calculated as

$$\mathrm{Var} = \frac{1}{|\Omega|}\int_\Omega \left(L(\mathbf{x}) - \mu_L\right)^2 \mathrm{d}\mathbf{x}, \quad \mu_L = \frac{1}{|\Omega|}\int_\Omega L(\mathbf{x})\mathrm{d}\mathbf{x}, \tag{2}$$

where $|\Omega| = 1$ is the area of the landscape. We normalize each landscape to satisfy $\mu_L = 1$. The landscape ACL measures how quickly the landscape varies from point to point, with large ACL corresponding to landscapes with large patches of similar landscape values and small ACL corresponding to small such patches (see Fig. C.1 for examples). We calculate the landscape ACL using Moran's I (see Appendix A for details).

The landscape values $L(\mathbf{x})$ govern the local growth of the autotroph by setting the growth rate of the autotroph, $g(\mathbf{x})$, and its carrying capacity $K(\mathbf{x})$ to equal $g_0 L(\mathbf{x})$ and $K_0 L(\mathbf{x})$, respectively. Thus, high landscape values represent favorable locales for the autotroph, and low landscape values represent unfavorable locales. In a natural system, such variations could, for example, come about through spatial variation in resource supplies of, e.g., phosphorus or nitrogen, spatial temperature gradients, or variations in depth in aquatic ecosystems. For simplicity, we do not consider scenarios where the intrinsic growth and the carrying capacity of the autotroph are governed by different resource landscapes (e.g., growth by temperature and carrying capacity by rainfall).

Write $u_0^*(\mathbf{x})$ for the autotroph density in Eqs. (1) at eco-evolutionary equilibrium in the fully evolved community. We take $G_A(\mathbf{x}) := g(\mathbf{x})u_0^*(\mathbf{x})$ to be the measure of the local autotroph productivity, and by adjusting g_0 and K_0 we can normalize the total autotroph productivity $\int_\Omega G_A(\mathbf{x})\mathrm{d}\mathbf{x}$ in the fully formed evolutionarily stable community for all generated landscapes $L(\mathbf{x})$. This normalization is not perfect, but varies less than 1% among outcomes (see Appendix A for details).

2.3. Evolutionary dynamics

We assemble evolutionarily stable communities under the assumption that the relative logarithmic body sizes of heterotrophs, r_i, are evolvable traits. We use adaptive-dynamics methods to compute the evolutionary dynamics of the system. Following the methods of Wickman et al. (2017), we calculate the selection gradient for each trait, $\mathscr{D}(r_i)$, which is a measure of the strength and direction of directional selection acting on the traits r_i . To solve for the effects of directional selection on the heterotrophs we add one ordinary differential equation for each heterotroph,

$$\frac{\mathrm{d}r_i}{\mathrm{d}t} = \epsilon\mathscr{D}(r_i), \tag{3}$$

describing how traits evolve over time due to directional selection. Here ϵ is a number that is small enough for Eqs. (1) to be close to ecological equilibrium at all times, meaning that ϵ separates the ecological and evolutionary time scales.

The evolutionary community assembly process proceeds by the following steps: (1) The process starts with a single heterotroph with $r_1 = 1$ and the autotroph both homogeneously distributed in space. (2) We integrate all heterotrophs to eco-evolutionary equilibrium, i.e., $\mathscr{D}(r_i) = 0$ for all heterotrophs. (3) We compute the fitness landscape in trait space, and if a region with positive invasion fitness exists, we add a new heterotroph with maximal invasion fitness to the system with a small uniform density. (4) We repeat steps 2–3 until no more regions of trait values with positive invasion fitness are available.

Fig. 1 shows an example of an evolutionary community assembly process for a given resource landscape. In this example, we use an evolutionary branching process (see Appendix A) to be able to exemplify some facets of our analysis of disruptive selection at the first evolutionary branching point. As stated in the steps above, we carry out the actual simulations by letting invaders with maximal invasion fitness enter the ensemble. We do so for two reasons. First, since we are primarily interested in the final evolutionarily stable communities, we use this method as it significantly reduces the numerical computation time for each outcome. Second, sometimes the evolutionary branching process will not fill all available niche space, and the community has to be closed by invasion of mutants at fitness peaks regardless. All generated food webs appear to be unique eco-evolutionary attractors for the corresponding resource landscape, so that each landscape corresponds to exactly one specific fully formed food web. Experiments with varying the starting conditions, as well as randomly removing heterotrophs from a fully formed food web and then reforming it yielded no alternative stable states among the roughly 100 out-

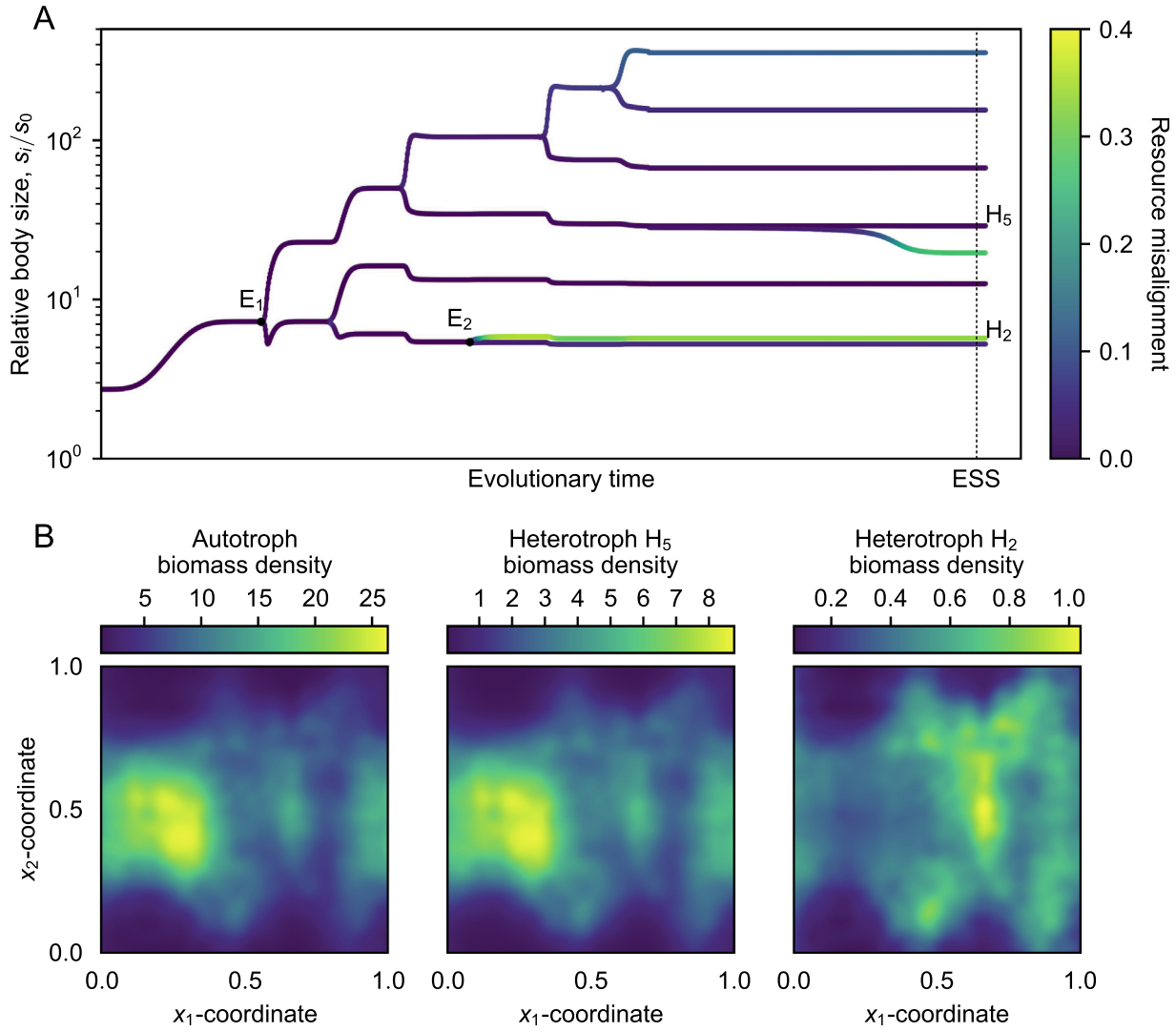

Fig. 1. Example of evolutionary community assembly for a given landscape. (A) Evolution of heterotroph relative size compared to the autotroph, s_i/s_0, over time, with a single ancestral heterotroph evolving into an evolutionarily stable community of eight heterotrophs. The colors of the lines indicate the resource misalignment of the heterotroph. H_2 and H_5 cross-reference the spatial distributions in panel B. E_1 and E_2 indicate 'sympatric' and 'parapatric' evolutionary branching points, respectively (see Figs. C.4 and C.5 for additional details). (B) Spatial density distribution of the autotroph and two heterotrophs. Heterotroph H_5 has a very low degree of resource misalignment, and has almost the same spatial distribution as the autotroph. Heterotroph H_2 has a high degree of resource misalignment, meaning that its spatial distribution is different from the autotroph's.

comes we tested. We believe that the reason for the lack of priority effects, i.e., that the order in which the food web is assembled does not matter, is due in large part to our assumption that the entire trait space is available for invasions. Limited experiments with allowing only small mutations did sometimes yield different food webs depending on initial conditions, but such food webs always had unexploited trait space available globally after the food web had finished assembling by small mutations. That is, incremental evolution through small mutations can lead to alternatively structured food webs, exhibiting priority effects and accompanied by empty niches in trait space waiting to be invaded.

Additional details on how the evolutionary community assembly is carried out can be found in Appendix A.

2.4. Data analysis

To see how resource-landscape variance and autocorrelation length (ACL) affect properties of the evolved food webs, we assemble 4632 communities with landscape variance in the interval $(0, 0.6)$ and ACL in the interval $(0.1, 0.3)$. We choose these ranges as they generally yield landscapes for which evolutionary community assembly is numerically feasible, while still covering a large range of different landscapes. Examples of the types of landscapes corresponding to high and low variance and ACL can be found in Fig. C.1. We picked the values of landscape variance and ACL uniformly at random; a scatter plot of the landscape variances and ACLs is depicted in Fig. C.3.

To visualize the effects of landscape variance and ACL on a property (dependent variable) of interest, we use a scatter plot of the dependent variable z against the landscape variance L_{VAR} and the landscape ACL L_{ACL} to create a smoothed plot of the mean of the dependent variable $\mu_z(L_{\mathrm{VAR}}, L_{\mathrm{ACL}})$ by smoothing the scatter plot using local regression (LOESS, see Cleveland, 1979; Cleveland and Devlin, 1988). We use this method to generate Figs. 2–4. Additional details can be found in Appendix B.

As heterotrophs in the model can be omnivorous, the trophic levels of heterotrophs are fractional and are calculated based on the proportion of consumption of other heterotrophs and the autotroph (Odum and Heald, 1975; Williams and Martinez, 2004). See Appendix B for details.

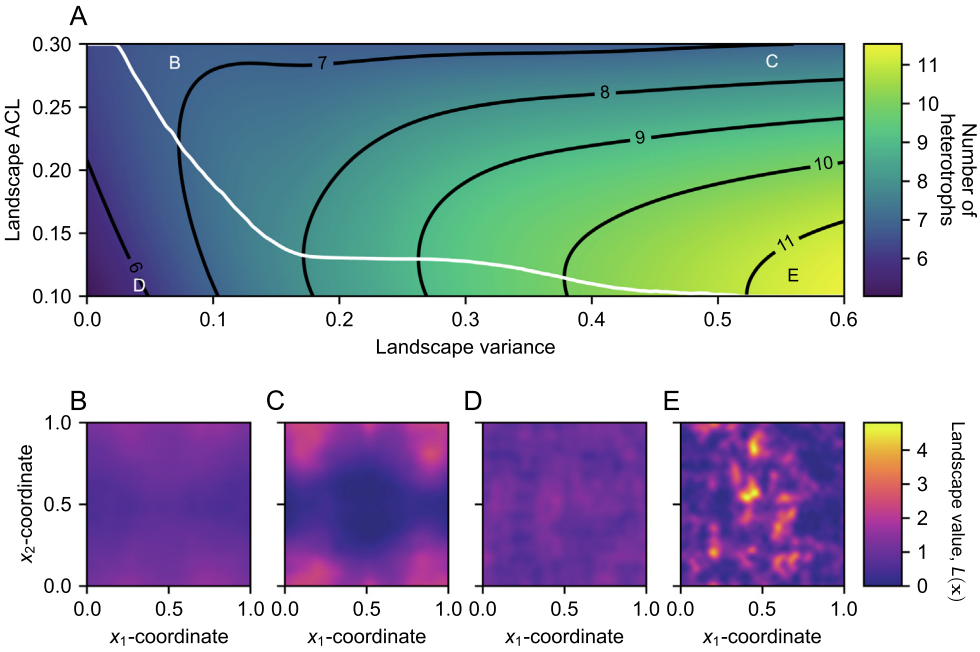

Fig. 2. Diversity increases with landscape variance and is unimodal in autocorrelation length (ACL). (A) Average number of evolved heterotrophs in the food web plotted against landscape variance and ACL. The white line indicates the ACL that maximizes average diversity for each given landscape variance. The letters B-E in the panel cross-reference examples of resource landscapes $L(\mathbf{x})$ for different degrees of landscape variance and ACL, with (B) low variance and high ACL, (C) high variance and high ACL, (D) low variance and low ACL, and (E) high variance and low ACL. Note that all landscapes are periodic in both spatial dimensions. Additional examples of productivity landscapes can be seen in Fig. C.1.

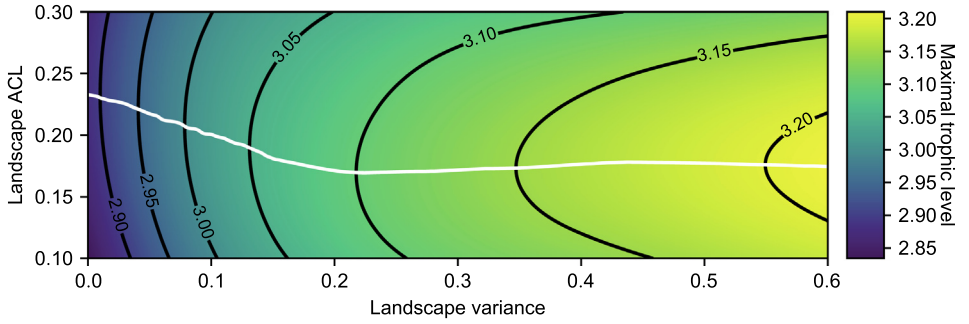

Fig. 3. Trophic level increases with landscape variance and is unimodal in autocorrelation length (ACL). Average maximal trophic level in the food web plotted against landscape variance and landscape ACL. The white line indicates the ACL that maximizes average maximal trophic level for each given landscape variance.

In order to better understand how heterotrophs are distributed in space, we calculate a dissimilarity measure between each heterotroph's spatial distribution and the autotroph's on the same landscape. We base this measure on the Kendall rank correlation coefficient, which we transform to an increasing measure $d_k \in [0, 1]$, with heterotrophs with d_k close to zero having the most similar spatial distributions to the autotroph and heterotrophs with d_k close to one having the most different spatial distributions. As d_k measures the degree to which a heterotroph deviates from the autotroph's spatial distribution, we call d_k the degree of resource misalignment. See Appendix B for additional details.

To analyze how properties of the evolved food web compare to properties of the initial evolutionary branching event (e.g., point E_1 in Fig. 1), we follow Wickman et al. (2017) and separate the stabilizing/disruptive selection at an evolutionarily singular point into two terms (see Wickman et al., 2017, Eq. (B5)). The first term, 'sympatric selection', is a weighted average of the curvature of the fitness landscapes at all points in space. The second term, 'parapatric selection', is, roughly speaking, the weighted variance of directional selection over all points in space, where the weights in both terms depend on the heterotroph's spatial density distribution. These different types of disruptive selection tend to, depending on which term is dominant, engender different kinds of evolutionary branchings, exemplified in Figs. C.4 and C.5. 'Sympatric' branchings, where the first term is dominant, lead to two new heterotrophs with the same spatial distribution as their ancestor, and 'parapatric' branchings, where the second term is dominant, lead to two new heterotrophs, of which one has a different spatial distribution than its ancestor.

3. Results

Using resource-landscape variance and autocorrelation length (ACL) as predictors, we investigate three properties of the evolved food webs. These are the diversity, as measured by the number of heterotrophs, the maximal trophic level, and the resource misalignment, i.e., the degree to which heterotrophs' spatial distributions differ from the autotroph's in the same outcome. We then examine how well these properties can be predicted from proper-

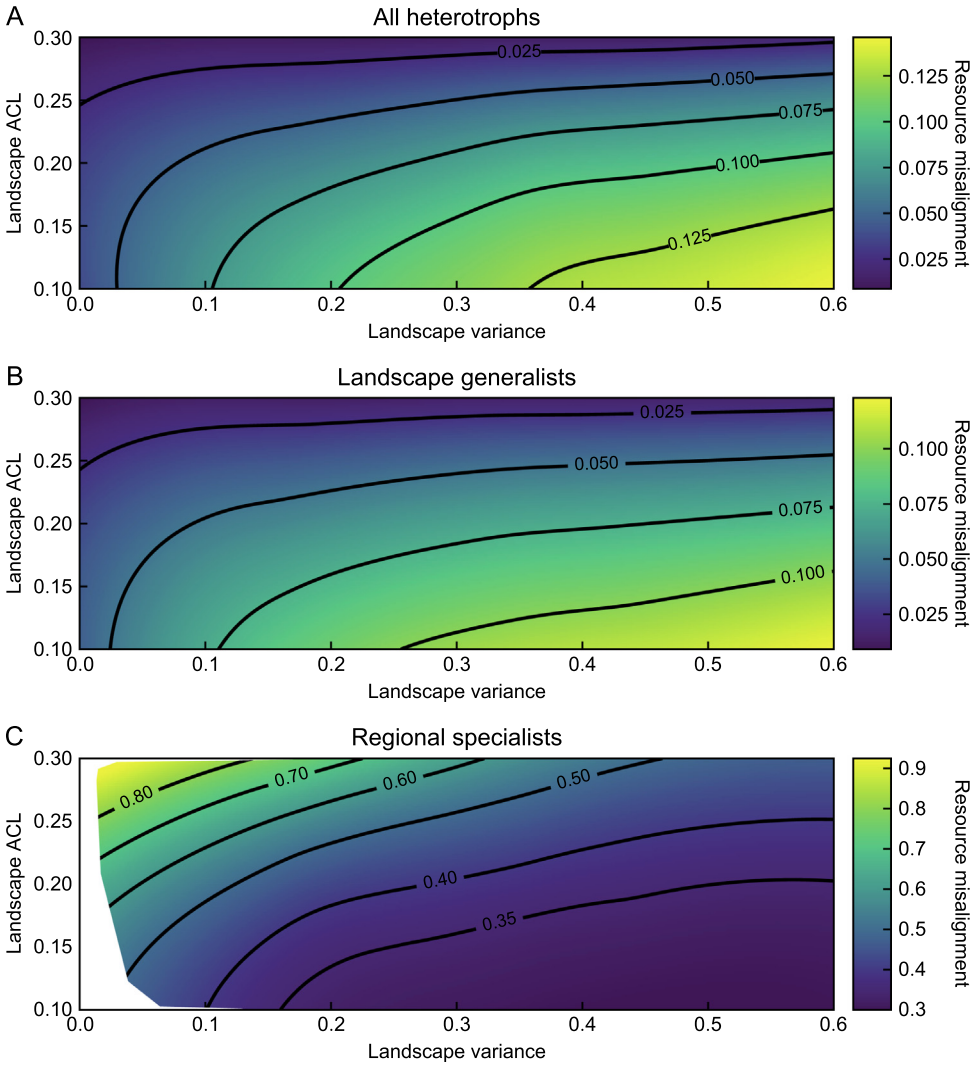

Fig. 4. The degree of resource misalignment among heterotrophs depends on whether the heterotroph is a landscape generalist or regional specialist. (A) Average resource misalignment increases with landscape variance and decreases with autocorrelation length (ACL). Average degree of resource misalignment among all heterotrophs plotted against landscape variance and landscape ACL. In contrast to diversity and maximal trophic level, which are properties of each outcome, the average here, using LOESS regression, is taken over all (38504) heterotrophs among all evolved outcomes. (B) For landscape generalists, resource misalignment is promoted by high landscape variance and low ACL. Average degree of resource misalignment among landscape generalists in the food web plotted against landscape variance and ACL. (C) For regional specialists, resource misalignment is promoted by low landscape variance and high ACL. Average degree of resource misalignment among regional specialists in the food web plotted against landscape variance and ACL. For outcomes with very low variance there are no regional specialists, and we have cut the figure along the convex hull of outcomes. See Appendix B for details on the classification of heterotrophs into landscape generalists and regional specialists.

ties of the first evolutionary branching event in the formation of the food web.

3.1. Diversity increases with landscape variance and is unimodal in autocorrelation length

Fig. 2 shows the average number of heterotrophs in the evolved food web for different levels of landscape variance and ACL. Diversity increases with variance, and for each variance, the average diversity is maximized at an intermediate ACL. The ACL that maximizes diversity decreases as the variance increases, so that landscapes with low variance require a high ACL for maximal diversity, whereas landscapes with high variance require a low ACL to maximize diversity. Conversely, low ACL implies that diversity increases rapidly as variance increases, whereas the increase in diversity with increased variance is slow if ACL is high. The minimum number of heterotrophs among all outcomes is 5, and the maximum is 14.

To understand the results pertaining to diversity, note that although the prey trait difference that maximizes the predator's attack rate μ_γ is a constant that is the same for all morphs across the landscape, different local productivities will nevertheless have different trait values that are optimally adapted to that productivity. This is because the consumption and respiration terms in the equations governing the heterotroph dynamics (Eq. (1a)) both depend on the trait value and will respond differently to different levels of autotroph productivity. In the absence of diffusion, each point in space would thus have a particular local food web adapted to the local productivity conditions.

3.2. Trophic level increases with landscape variance and is unimodal in autocorrelation length

Fig. 3 shows the average maximal trophic level among the evolved food webs for different levels of landscape variance and ACL. In contrast to the number of evolved heterotrophs, the differ-

ence among outcomes for maximal trophic level is not great, with the smallest maximal trophic level being 2.83 and the largest maximal trophic level being 3.34. The maximal trophic level increases with landscape variance and is maximized at an intermediate ACL. For higher variances, the ACL that maximizes trophic level is higher than that which maximizes diversity. We discuss this discrepancy further in the discussion section.

The maximal trophic level is strongly correlated with how big the biggest heterotroph in the system is (Fig. C.2). Although the difference in maximal trophic level is small, the differences in size between the biggest heterotrophs among all outcomes are more significant, with the largest largest heterotroph being 3.78 times bigger than the smallest largest heterotroph.

3.3. Resource misalignment increases with variance and decreases with autocorrelation length

Fig. 4A shows the average resource misalignment among the heterotrophs for different levels of landscape variance and ACL. The average degree of resource misalignment is nearly strictly increasing with variance and decreasing with ACL. To further understand how the resource misalignment differs between heterotrophs, we explore the distribution of resource misalignment at different trophic levels and find that the distribution is typically bimodal with a clear separation into 'landscape generalists'—whose spatial distributions are aligned with the autotroph's—and 'regional specialists'—whose spatial distributions are misaligned with the autotroph's—except at the highest trophic level, at which all heterotrophs can be considered landscape generalists (see Appendix B).

Fig. 4B shows the average degree of resource misalignment for the landscape generalists in the food web. The degree of resource misalignment for each outcome is based on the average of all generalist heterotrophs. The resource misalignment is nearly strictly increasing in variance and decreasing in ACL. The outcome with the lowest resource misalignment has a resource misalignment of 0.0057, and the outcome with the highest resource misalignment has a resource misalignment of 0.16. Most emerged heterotrophs are landscape generalists; as such, the resource misalignment of a typical heterotroph (Fig. 4A) largely reflects that of a landscape generalist (Fig. 4B)

Fig. 4C shows the average degree of resource misalignment for regional specialist heterotrophs in the food web. The resource misalignment for each outcome is based on the average of all regional specialists. The resource misalignment is nearly strictly decreasing in variance and increasing in ACL. The outcome with the lowest resource misalignment has a resource misalignment of 0.10, and the outcome with the highest resource misalignment has a resource misalignment of 0.92. For outcomes with very low landscape variance, there are no regional specialists, resulting in the white area to the left in Fig. 4C, where we cut the surface resulting from LOESS regression along the convex hull of the outcomes containing at least one regional specialist.

Taken together, Fig. 4 shows that for low landscape variance and high ACL the distribution of resource misalignment is strongly bimodal with most heterotrophs being spatially very similar to the autotroph, but with a smaller number of highly misaligned heterotrophs. Moving along the diagonal of Fig. 4 from the upper left to the lower right, this pattern is gradually replaced by a unimodal distribution, where the typical heterotroph has a higher degree of resource misalignment. This pattern can be understood in the following way. When landscape variance is low, large patches of low or intermediate productivity are required in order for a regional specialist to survive, and the low landscape variance–high ACL regions of parameters tend to generate such patches completely distinct from the distribution of the autotroph, resulting in regional specialists that are highly misaligned with the autotroph. With high landscape variance, local productivity differs more from place to place, and as such there are more ways in which heterotrophs may adapt their spatial distributions without having to be completely misaligned with the autotroph. However, the competition between partially overlapping heterotrophs tends to ensure that few heterotrophs can be completely aligned with the autotroph.

3.4. Regional specialists have lower biomass and trophic level than landscape generalists

The typical characteristics of the regional specialists differ from the landscape generalists in several respects. As the spatial distributions of regional specialists are not aligned with the primary production in the system, they tend to have significantly lower total biomass compared to the landscape generalists, and among all heterotrophs total biomass tends to decrease as resource misalignment increases (Fig. C.6). This also means that most regional specialists tend to be small heterotrophs with low trophic level, as the lower productivity levels where the regional specialists reside cannot support long food chains (Fig. B.2). When landscape variance and ACL are low, regional specialists tend to be more spatially aggregated than the landscape generalists, and when landscape variance and ACL are high, regional specialists tend to be less spatially aggregated than the landscape generalists (Fig. C.8). The part of parameter space where regional specialists are less aggregated is nevertheless bigger, as the areas of the landscape away from where specialists are best adapted have higher levels of productivity, which counteracts aggregation. Similarly, when landscape variance and ACL are low, the ACLs of the regional specialists' spatial distributions tend to be higher than those of the generalists, and when landscape variance and ACL are high, the ACLs of the regional specialists' spatial distributions tend to be lower than those of the generalists (Fig. C.9). These patterns can be understood by the fact that regional specialists reside on the complement of the range of the generalists, which naturally tend to have the opposite characteristics. There are also, however, a small number of highly misaligned regional specialists across landscape variance–ACL space that are highly aggregated in a small part of the landscape, which do not follow the aforementioned general pattern.

3.5. Components of initial disruptive selection predict properties of the evolved community

To measure the degree to which we can predict the properties of the evolved community using the components of the initial disruptive selection we carry out a linear regression for diversity and maximal trophic level against the components of disruptive selection, and a logistic regression for the resource misalignment of landscape generalists. Fig. 5 shows how properties of the evolved communities depend on components of disruptive selection for the first evolutionary branching point (e.g., point E_1 in Fig. 1), with the corresponding regressions given in the figure caption. We now describe each panel in turn.

First, Fig. 5A shows that both sympatric and parapatric disruptive selection correlate positively with high diversity, with both factors being of approximately equal importance. This conclusion is also supported by hierarchical partitioning (Chevan and Sutherland, 1991), by which 54% of the variance explained by the regression is explained by sympatric disruptive selection and the remaining 46% by parapatric disruptive selection. Next, Fig. 5B shows that primarily sympatric disruptive selection correlates positively with higher maximal trophic level, with 69% of the explained variance explained by this factor. Finally, Fig. 5C shows that both sympatric and parapatric disruptive selection correlate positively with

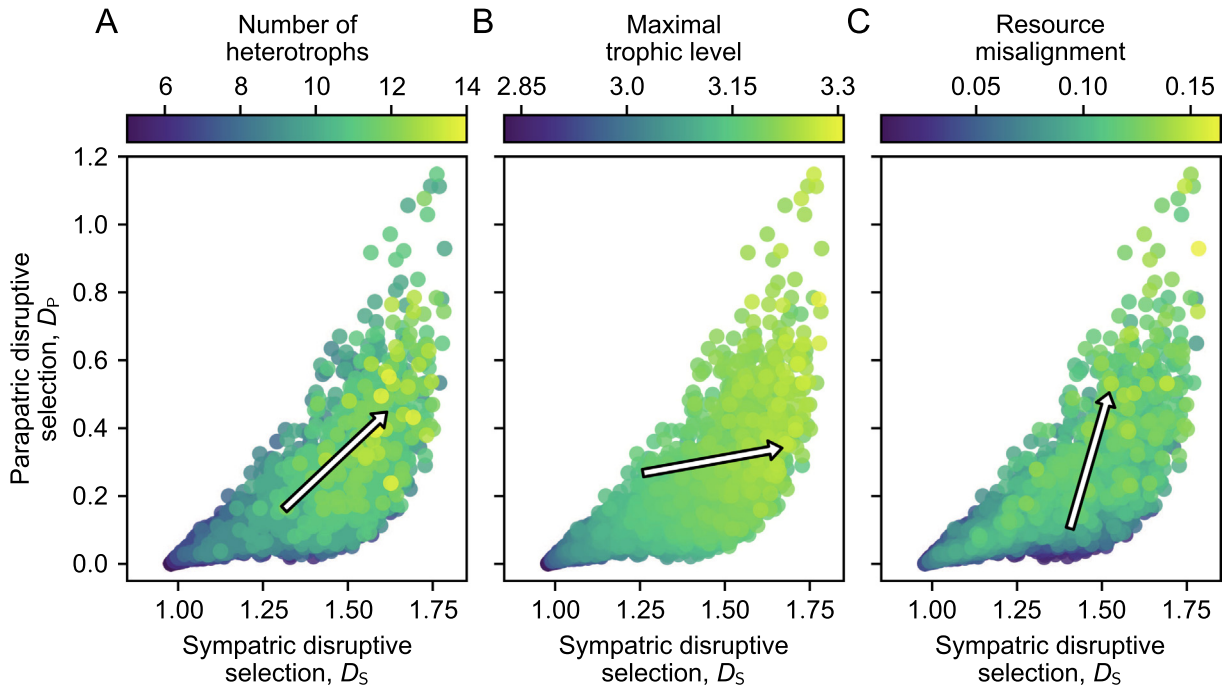

Fig. 5. Components of initial disruptive selection predict properties of the evolved community. Properties of the evolved communities plotted against the components of the disruptive selection experienced by the ancestral heterotroph. The total disruptive selection D_T of the ancestral heterotroph is the sum of sympatric disruptive selection D_S and parapatric disruptive selection D_P, so that $D_T = D_S + D_P$ (see methods section). Higher values are plotted on top of lower values. In all panels, the arrows show the direction of the gradient of a regression, indicating the direction of maximum increase. (A) Number of heterotrophs in the evolved community. (B) Maximal trophic level in the evolved community. (C) Average resource misalignment among landscape generalists in the evolved community. We have removed four outliers in the explanatory variables from the analysis. Letting z be the dependent variable, D_S the sympatric disruptive selection, and D_P the parapatric disruptive selection, we compute the gradients from the following regressions. A: $z = 2.4 + 4.0D_S + 4.3D_P$ $(r^2 = 0.63)$. B: $z = 2.6 + 0.38D_S + 0.069D_P$ $(r^2 = 0.82)$. C: $\text{logit}(z) = -3.6 + 0.47D_S + 1.6D_P$ $(r^2 = 0.41)$, where r^2 in the regression for C is based on the predictive residuals from leave-one-out cross-validation.

resource misalignment for landscape generalists, but that parapatric disruptive selection is the stronger predictor with 63% of the explained variance explained by this factor. The resource misalignment z of the regional specialists is described by the regression $\text{logit}(z) = -1.9 - 1.4D_S - 1.2D_P$, $r^2 = 0.37$ (data not shown).

4. Discussion

4.1. How diversity is structured in spatially heterogeneous evolved food webs

While the consequences of varying levels of mean productivity on diversity have been extensively studied (Adler et al., 2011; Cusens et al., 2012; Mittelbach et al., 2001), the effects of altering the variance of productivity is much less well understood, although it has been hypothesized to increase diversity (Scheiner and Willig, 2005; Willig, 2011). Our results, as shown in Fig. 2, support this hypothesis, although the rate of increase depends on the autocorrelation length (ACL) of the resource landscape. In general, the link between diversity and environmental heterogeneity of various kinds is an active research field, and in their review on the topic Stein and Kreft (2015) cautioned that productivity may be confounded with heterogeneity as, e.g., high-productivity areas may also harbor a more heterogeneous mix of plants. However, direct studies of the effects of heterogeneous levels of productivity are, as far as we can tell, scarce. The one empirical study by Gundale et al. (2011) on the relationship among diversity, productivity, and resource heterogeneity we have been able to find contrasted with our finding that more heterogeneous productivity gave rise to more diverse communities. They found no link between soil resource variability and the productivity–diversity relationship in understory plant communities, although they focused on the variation in the mix of several resources, rather than the variation of productivity, and did not consider several trophic levels.

When productivity is heterogeneously distributed in space, it affects the local trophic dynamics, with pockets of higher productivity promoting local, longer, and more complex food chains. The heterogeneous distribution also creates the opportunity for local adaptation, as different trait values are differentially adapted to areas with high, medium, and low productivity. As variance increases, the differences between parts of the landscape become increasingly pronounced, as well as providing patches of increasingly high local productivity. For diversity this has the effect that for low variance highly correlated landscapes are required for diversification. Since the differences in productivity levels across the landscape are small, larger patches of similar levels of productivity are required both for local adaptation, i.e., the critical patch size is larger (see, e.g., Cantrell and Cosner, 2004), as well as sustaining a locally bigger food web. As variance is increased and productivity conditions become increasingly more different, patch size becomes less of a critical factor. Instead, having higher peaks in the resource landscape and having better separated different conditions become important, which are both features of low ACL. As seen in Fig. 2, the average diversity roughly doubles between the least and most diverse outcomes. This is large enough to be significant compared to studies that investigated the effects of the overall productivity on food-web diversity (Steiner and Leibold, 2004), and empirical studies (Adler et al., 2011; Chase and Leibold, 2002; Cusens et al., 2012). This suggests that not only is choosing the spatial scale of measurement important for understanding the productivity–diversity relationship (Chase and Leibold, 2002; Steiner and Leibold, 2004), but that having a good idea of the spatial structure of productivity is as well.

The maximal local trophic level is much less sensitive to how productivity is distributed in the landscape (Fig. 3). Maximal food-chain length is thought to be positively related to productivity (Takimoto and Post, 2013), and a small effect of having larger local productivity at some points in the landscape is evident for landscapes with higher variance. We also find that for high landscape variances, trophic level is maximized by higher landscape ACL compared to diversity (Figs. 2 and 3). This can be understood primarily through two factors, both related to dispersal: First, as larger heterotrophs diffuse more quickly than smaller heterotrophs and food-web size is highly contingent on the size of the largest heterotroph in the web, larger patches are required to sustain the larger heterotrophs. Second, there is likely an effect of compound dispersal at play, with all heterotrophs below the largest heterotroph in the food web diffusing out of the highest productivity areas, requiring a larger patch to sustain the largest heterotroph without too much of its prey being lost to diffusive losses into maladapted areas. This phenomenon is also related to the idea that spatial structure can be viewed from the perspectives of both heterogeneity and fragmentation (Laanisto et al., 2013; Tews et al., 2004). For the very largest morphs, the landscapes with the highest variance and smallest ACL are too fragmented to support them, but for the smaller morphs, these landscapes provide the right amount of heterogeneity to support a high total diversity.

Since the differences in maximal trophic level are modest between outcomes, and the principle of competitive exclusion (Gyllenberg and Meszéna, 2005; Levin, 1970; Meszéna et al., 2006) dictates that heterotrophs should be separated sufficiently far in trait space in order to coexist, the primary way in which additional heterotrophs may coexist is for them to be spatially differentiated from the spatial structure set by the resource landscape. The way in which heterotrophs become spatially dissimilar depends on the variance and ACL of the underlying resource landscape. As variance increases and ACL decreases, the spatial dissimilarity of a typical heterotroph increases (Fig. 4A), but the most spatially dissimilar heterotrophs are found when variance is low and ACL is high (Fig. 4C). As can be seen in Fig. 4B and C, in which heterotrophs with high and low degrees of dissimilarity are considered separately, this engenders a scenario where low variance–high ACL landscapes generate food webs with heterotrophs either distributed very similarly to the autotroph or very differently. In contrast, high variance–low ACL landscapes generate food webs with most heterotrophs being at least moderately different from the autotroph, but no one heterotroph being completely dissimilarly distributed. This can be understood as in the low variance–high ACL scenario, where there will typically be only two different types of productivity patches with little spatial overlap, resulting in some locally adapted heterotrophs distributed away from high density areas of the autotroph. In the high variance–low ACL scenario, the more distinct and well separated conditions allow for less drastic spatial differentiation from the autotroph among the heterotrophs, but competition between partially overlapping heterotrophs tend to separate heterotrophs away from exactly following the autotroph's spatial distribution.

4.2. Predicting evolved diversity from initial disruptive selection

While spatial evolutionary food-web studies are rare, several authors have investigated under what conditions spatial structure promotes evolutionary branching (Doebeli and Dieckmann, 2003; Mágori et al., 2005; Parvinen et al., 2017). Haller et al. (2013), in particular, studied the effects of landscape structure on evolutionary branching in complex landscapes similar to those studied here, with the landscapes describing the optimal ecological character for an ecotype to maximize its carrying capacity in an individual-based model. They found that an intermediate landscape variance maximized the propensity for branching, which seems to contrast with our finding that diversity increases with landscape variance. However, as shown by Brännström et al. (2011), the food-web model studied here may undergo evolutionary branching in the absence of spatial structure, and propensity for branching need not coincide with maximal diversity.

Here we have examined to what extent such results concerning the propensity for evolutionary branching can be extended to be used as predictors of properties of an evolutionarily stable community in a food-web setting. We calculated two components of disruptive selection, of which the first corresponds to an average of local stabilizing/disruptive selection (sympatric selection) and the second takes into account how spatial heterogeneity contributes to disruptive selection by providing different directional selective regimes at different locations (parapatric disruptive selection). Fig. 5A shows that both components predicted diversity equally well, with predicted diversity increasing with increases in these components. This contrasts with the results for the maximal trophic level (Fig. 5B), where the predictive power of the two components of disruptive selection is greater than that for diversity and is contributed predominately by the sympatric component. The local maximal trophic level is only contingent on how big a local food web can be evolved, which is not dependent on the degree to which resource misalignment was prevalent. This is reflected already at the stage of initial disruptive selection as the propensity for the first heterotroph to branch into different spatial configurations, as measured by parapatric disruptive selection, does not factor in predicting the maximal trophic level of the evolved food web.

Conversely, the resource misalignment among landscape generalists is more strongly predicted by the amount of initial parapatric disruptive selection (Fig. 5C), although the effect of sympatric disruptive selection is a stronger predictor than parapatric disruptive selection is for maximal trophic level. This may be due to the fact that as the size of the food web becomes greater, it also allows for larger as well as smaller heterotrophs to branch out spatially. The pattern for the degree of resource misalignment among regional specialists is not as straightforwardly reflected in the initial disruptive selection, and the most misaligned regional specialists tend to occur in systems where initial disruptive selection of both kinds is weak.

Taken together, our results indicate that initial disruptive selection is a reasonably good predictor of several properties of the evolved community in a food-web model, which in turn suggests that knowing spatial properties of the resource landscape engenders better predictive power from the initial disruptive selection than what was found when the parameters of biotic interactions in a corresponding nonspatial model were varied (Brännström et al., 2011). While this is encouraging in that it suggests that results from spatial studies concerning evolutionary branching might also provide some insight into properties of a fully formed community, some care should be taken not to overly generalize. First, evolutionary diversification in heterogeneous landscapes may occur even when sympatric selection is stabilizing (Wickman et al., 2017). Second, the quantity we vary in space is strictly positive, which means that a distribution with given variance and ACL can look quite different from a distribution that does not need to be positive but exhibits the same variance and ACL. An example of the latter would be the system studied by Haller et al. (2013), where an optimal ecological character was varied through space. The comparison with this study cautions that one should take care when specifying what one means by environmental heterogeneity, as the consequences for diversity might be quite different.

4.3. Model limitations and future extensions

In our model we have made the assumptions that dispersal is random and that the rate of random dispersal of individuals scales positively with body size according to a power law (Peters, 1983), and our results are partially contingent on these assumptions. Incorporating preferential movement towards more profitable locations—through, e.g., gradient dynamics such as chemotaxis or 'good-stay, bad-leave' behaviors—would likely allow both slightly longer food chains to form, as top predators would need smaller patches to survive, as well as increase the ability of morphs to adapt locally by limiting their dispersal. It is, however, not a priori clear whether incorporating such mechanics would yield significant differences when compared to an overall lowering of the base dispersal rate in the ecosystem, and a formal study of these points would make an interesting extension of the results we present here.

We have restricted our study to evolutionarily stable communities (ESCs), which are fully-, but not over-saturated. In essence, this means that we have explored the niche capacity for a given productivity landscape, i.e., the maximal diversity that can persist unchanged over evolutionary time scales. Although such communities will not always correspond to communities found in nature, they nevertheless yield important information on what types of communities are possible (Edwards et al., 2018). For example, by studying the fitness landscape of a given ESC (see Fig. A.1 for an example), one could qualitatively theorize about which parts of the trait space might be robust against the inclusion of neutral processes such as drift that can cause fluctuations in traits and densities for especially rare morphs (potentially regional specialists).

We observed in all our numerical outcomes that each resource landscape corresponded to precisely one ESC. We believe that this is primarily due to two factors. First, we have studied ESCs that are globally stable, i.e., closed to invasion by any conceivable trait value. If only local stability—i.e., stability with respect only to small deviations from the trait values of the residents (incremental evolution)—is considered, several different stable communities are sometimes possible for some landscapes. Note that 'local' and 'global' stability here refer to mutations in trait space, and not physical space. Second, systems that exhibit several different stable states depending on priority effects in homogeneous environments may often exhibit only one stable state in heterogeneous environments (Chase, 2010; Fukami, 2015). This is due to the fact that, in a sense, the heterogeneous environment serves as a large set of different conditions so that different morphs can coexist by partitioning space, and consequently the resulting community will exhibit high levels of beta diversity, instead of the priority effect of multiple stable states in systems with homogeneous environments.

Many variations of the underlying nonspatial food-web model have previously been studied (see Fritsch et al., 2019, for a review), and many different facets have been explored, including virtually all parameters governing the interactions of the nonspatial model, as well as the evolutionary emergence of food webs by mutations of different sizes and the resulting transitory evolutionary dynamics. Although this is a relatively simple family of models, a complete exploration of the total variation of behaviors is not numerically feasible, and different studies have thus focused on varying selected aspects of the model. We chose in this paper to examine variations in the spatial structure of productivity landscapes and have only checked our parameter set for qualitative robustness with respect to small deviations in some key parameters (Appendix D), but we do believe that many of the phenomena we observed are at least qualitatively generalizable to a broader range of parameters. However, other parts of the parameter space might give rise to interesting behaviors such as evolutionary cycling, which we have not observed in the present study and which would imply that no ESCs exist.

While we have focused here on the effects of varying productivity patterns, there are several other ways of introducing spatial heterogeneity to the basic food-web model. Allhoff et al. (2015) studied a version of a nonspatial food-web model of Loeuille and Loreau (2005) on two or eight discrete patches and investigated the effects of different dispersal patterns on emerged food webs, while Bolchoun et al. (2017) studied the effects of the topology of small networks of patches on food-web evolution. An individual-based evolutionary food-web model for soil food webs, where a number of traits were allowed to evolve independently, has also been investigated by Moya-Laraño et al. (2014), but spatial evolutionary food-web assembly models are otherwise a hitherto mostly unexplored field. One interesting venue for extending our findings would be to explore how varying the size of the autotroph across space rather than productivity would lead to different results compared to the scenario considered in this paper. Such an approach would enable us to study the inverse of the problem we have studied here, i.e., how diversity affects productivity, or more broadly, ecosystem functioning. This question has already seen vast interest (Cardinale et al., 2011; Hooper et al., 2005), and while nonspatial food webs (Schneider et al., 2016) and the impact of spatial diversity patterns (Lamošová et al., 2010) on ecosystem functioning have been studied, it is not well understood how spatial primary producer diversity would affect evolutionary food-web formation. Ritterskamp et al. (2016) studied a nonspatial version of a food-web model with two resources, each with a fixed size, and found that the total biomass (a proxy for productivity) did vary as they varied the size difference between the two resources. However, as the focus of their study was not on the connection between diversity and productivity, their results do not provide much of a suggestion, beyond that diversity in the resources will indeed change the productivity of the evolved food web. One caveat of using our model with autotroph size varying in space is that one would need to consider a nonspatial model with the same size distribution for comparison, since in the limit of the well mixed case, there would still be autotrophs of different sizes on which the heterotrophs could feed. This complication does not arise in our study since a nonspatial distribution of autotroph productivity is functionally equivalent to a single autotroph variant with the total productivity of the distribution. As we have also normalized the total productivity of the autotroph across space, we have effectively introduced as little variation as possible, and our study can be seen as providing a lower bound on the effects of spatial heterogeneity on size-structured evolutionary food-web formation. We can thus expect that, in reality, the effects of environmental heterogeneity should be at least as pronounced as predicted here, providing a baseline of how communities might change if their habitat structure is altered.

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Author contributions

JW performed the mathematical and statistical analysis, wrote the code for the numerical analysis, participated in the conception and design of the study, and drafted the manuscript. UD, CH, and ÅB participated in the conception and design of the study, discussed the results, and helped draft the manuscript. All authors gave final approval for publication.

Data availability

The data for the fully formed food webs, as well as the code used to generate and analyze the data, is available through the Dryad Digital Repository at https://doi.org/10.5061/dryad.qz612jmbv.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary online appendices

Supplementary appendices associated with this article can be found, in the online version, at https://doi.org/10.1016/j.jtbi.2020.110374.

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